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Taxonomy of *Chlorospingus ophthalmicus* in Mexico and northern Central America

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Despite a broad latitudinal distribution, Neotropical humid montane forests ('cloud forests') are fragmented because they require specific environmental conditions, especially high humidity and altitude. Therefore, they occur in areas with steep slopes and high moisture input from clouds and mist (Brown & Kappelle 1995, Webster 1995). In Mesoamerica, cloud forests are highly fragmented, whereas in South America they constitute a more continuous band stretching 3,000 km through the Andes. Such characteristics make cloud forests intriguing (Foster 2001): this biome has witnessed the evolution of astonishing biological diversity, with large numbers of endemic taxa, many of them highly range-restricted (Fjeldså & Krabbe 1990, Gentry 1995, Hernández-Baños *et al.* 1995, Campbell 1999, Navarro *et al.* 2001). This diversity has been explained via hypotheses of how past climatic change affected cloud forests, provoking vertical and horizontal movements of different

magnitudes (Wijninga 1995), and permitting periods of relative isolation and of relative continuity of habitats (Graham 1993, Gentry 1995, Van der Hammen & Hooghiemstra 2001).

Common Bush-tanager *Chlorospingus ophthalmicus* is an emberizine finch (Yuri & Mindell 2002) that ranges from south and east Mexico south to Argentina in cloud forests and (to a limited extent) other humid montane forests (Isler & Isler 1987, Stotz *et al.* 1996; Fig. 1) and shrubbery (J. Fjeldså *in litt.* 2006). *C. ophthalmicus* has c.25 described subspecies, subdivided into eight morphotypes based on eye colour, presence of a pectoral band and of a postocular spot (Isler & Isler 1987). Only one such—the *ophthalmicus* group—occurs in Mesoamerica north of the Panamanian Isthmus, with as many as ten subspecies recognised, all with dark irides, a postocular spot and a pectoral band (Isler & Isler 1987; Fig. 1a).

Recent studies have demonstrated lack of gene flow amongst allopatric populations of this species using allozyme electrophoresis (Peterson *et al.* 1992) and mtDNA sequences (García-Moreno *et al.* 2004). The latter study addressed genetic differentiation amongst populations in Mexico and northern Central America. These works suggest that the ‘species’ is in fact a complex of species, an idea mentioned in several publications (Davis 1972, Howell & Webb 1995, Stotz *et al.* 1996, Navarro & Peterson 2004, García-Moreno *et al.* 2004). As no previous work has integrated views of morphological and genetic variation in clarifying species limits in the group, here we analyse geographic patterns of morphological variation in Mesoamerican *C. ophthalmicus* populations and compare these data with recent phylogenetic results (García-Moreno *et al.* 2004). The result is a reassessment of species limits in the group.

Methods

We measured and scored 355 adult specimens (233 males and 122 females) of *C. ophthalmicus* from Middle America. This material is deposited in the Instituto de Biología and Museo de Zoología of the Facultad de Ciencias, both Universidad Nacional Autónoma de México, Mexico City (UNAM), University of Kansas Museum of Natural History, Lawrence (KUNHM) and the Natural History Museum, Tring (NHM). Six morphometric characters and ten qualitative plumage coloration characters were analysed. Morphometric characters (abbreviations in parentheses) were: bill-length (BL), bill-width (BW) and bill-depth (BD; all three taken at the anterior edge of the nostril), wing-chord (WC), tail-length (TAIL) and tarsus-length to the lowest complete scute (TAR). Qualitative plumage characters scored were: the shape of the line in the forehead, crown colour, shape of the postocular stripe, throat colour, breast-band colour, throat pattern and presence of a whitish ‘ear’ and ‘eyebrows’ (see Appendix for details). All measurements were taken with digital callipers to the nearest 0.01 mm.

For analyses of geographic variation, we selected ten operational geographical units (OGUs), considering cloud forest continuity and disjunctions in Mexico and northern Central America (i.e., south to Nicaragua; Fig. 1b). For comparison with

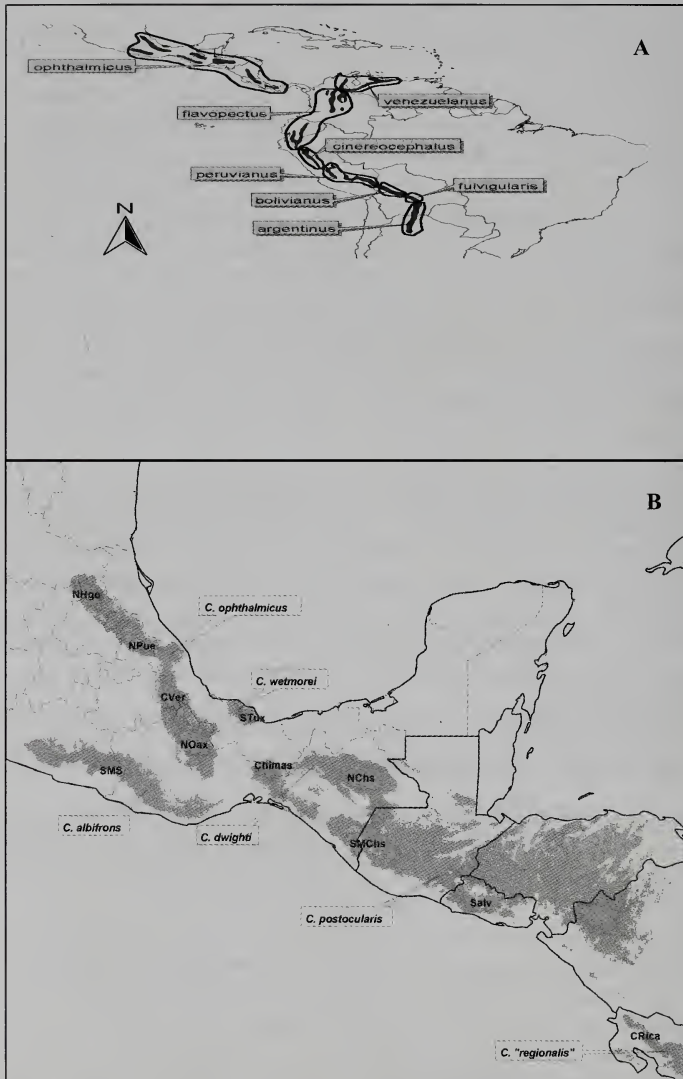


Figure 1a. Distribution of the *Chlorospingus ophthalmicus* complex showing the principal groups of Isler & Isler (1987); b: OGU and proposed species taxa of *Chlorospingus ophthalmicus* in Mesoamerica. Acromyns for OGUs are as follows: NHgo (south-eastern San Luis Potosi to northern Hidalgo), NPue (north-easternmost Hidalgo to northern Puebla), CVer (central Veracruz to extreme northern Oaxaca), NOax (northern Oaxaca), SMS (Sierra Madre del Sur, Guerrero and Oaxaca), STux (Sierra de los Tuxtlas, southern Veracruz), Chimas (Chimalapas region, eastern Oaxaca), NChs (northern Chiapas), SMChs (Sierra Madre de Chiapas, Pacific slope of Chiapas and southern Guatemala), Salv (El Salvador), and CRica (Costa Rica).

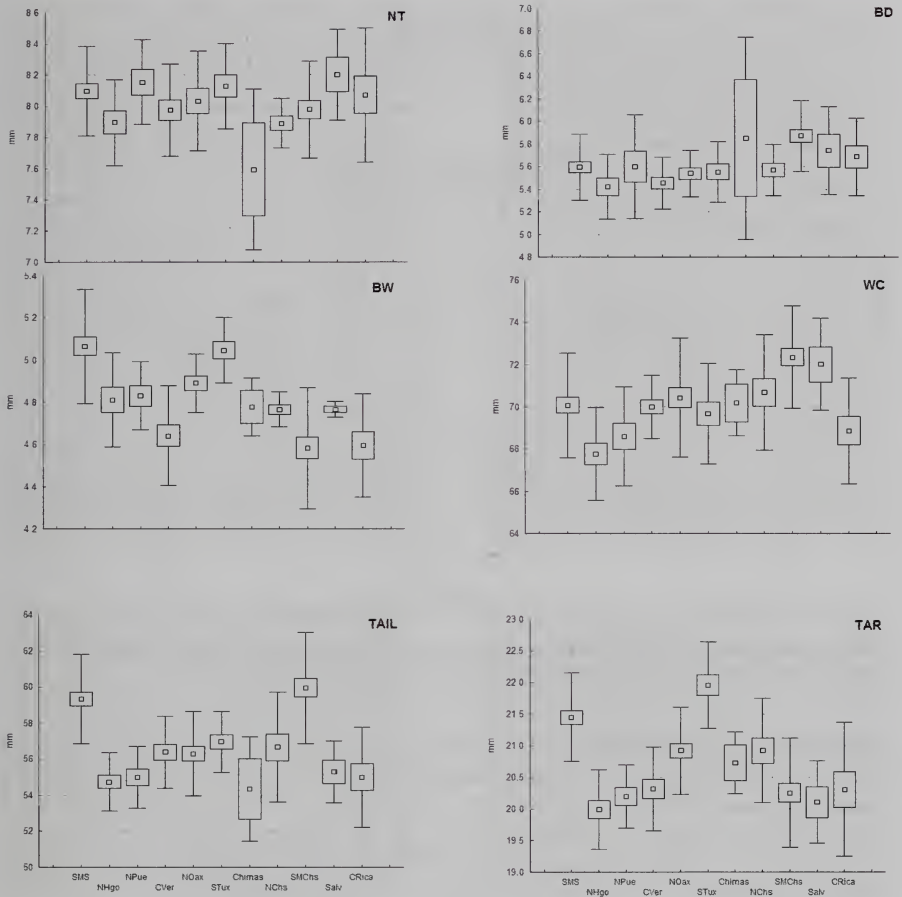


Figure 2. Variation in six morphometric characters. Shown are: means, standard errors (boxes) and standard deviations (whiskers). Characters depicted are: BL = bill-length from nostril; BD = bill-depth at nostril; BW = bill-width at nostril; WC = wing-chord; TAIL = tail-length; and TAR = tarsus-length. OGU acronyms refer to those used in Fig. 1b.

Chlorospingus populations further south, we included an additional OGU consisting of the subspecies *C. o. regionalis* (CRica), which occurs from northern Nicaragua to central Costa Rica; this OGU was chosen because of the large number of specimens available, and because it is the northernmost of the remaining populations. The geographic positions and abbreviations of OGUs are presented in Fig. 1b.

Morphometric characters were first evaluated using Pearson's product-moment correlations to detect redundant variables (Zink & Remsen 1986). Normality of

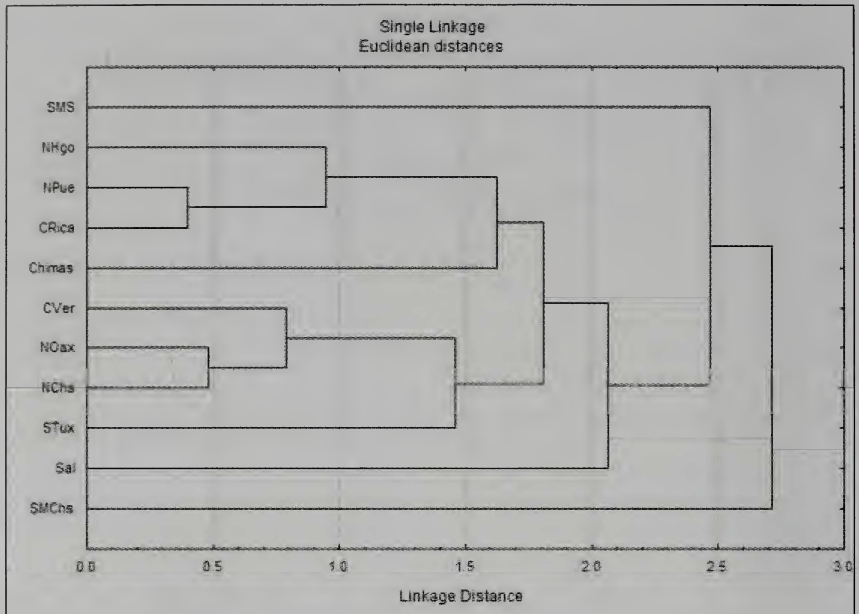


Figure 3. Phenogram (UPGMA) depicting patterns of overall similarity amongst populations of *C. ophthalmicus* in Mesoamerica. OGU acronyms refer to those used in Fig. 1b.

distributions of morphometric characters was tested for each OGU using Kolmogorov-Smirnov tests. Significance of differences amongst sexes was tested using univariate ANOVAs. To illustrate broad trends, we used centroids for each OGU (Crisci & López Armengol 1983, Zink & Remsen 1986)—we then used UPGMA cluster analysis (Sneath & Sokal 1973) in NTSyS (Rohlf 1992) to develop branching diagrams summarising overall similarity, and principal component analysis (PCA) to identify principal groupings (Johnson 1980, Crisci & López Armengol 1983). All statistical analyses were performed in STATISTICA V. 4.5. (Statsoft 1998), with a significance criterion of $\alpha = 0.05$.

Human-visible sexual dichromatism (Eaton 2005) is absent (Ridgway 1902, Graves 1985, Peterson & Chalif 1987) in this group, a conclusion supported by initial inspection of our data and specimens, which revealed no consistent sexual differences. As a result, we combined all data in analyses of coloration. Coloration characters were standardised via reference to Smithe (1975). Coloration characters were scored via use of a reference series of specimens to represent each character state (Appendix). Results were arranged geographically for easier detection of clinal variation and character discontinuities, and morphological results were compared with patterns detected in the analysis of DNA sequence data (García-Moreno *et al.* 2004).

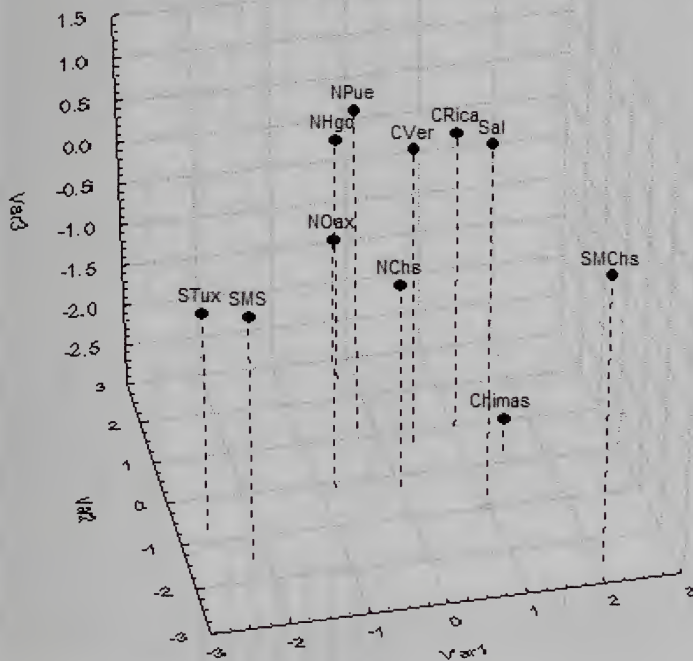


Figure 4. Principal Component Analysis of morphometric characters for the *C. ophthalmicus* complex in Mesoamerica. OGU acronyms refer to those used in Fig. 1b.

Results

Correlation coefficients indicated no redundancy between variables (highest $r = 0.067$), so all six morphometric characters were analysed. Kolmogorov-Smirnov tests revealed that all morphometric characters were normally distributed ($P < 0.05$). ANOVAs indicated significant sexual dimorphism in size (males average larger) in all populations except STux ($P < 0.05$), so all morphometric analyses were conducted for the two sexes separately. However, herein we present only results for males, given that results were similar for both sexes and that sample sizes were considerably smaller for females.

Morphometric characters that generally reflect body size (BL, WC, TAIL) showed clinal increases from north to south (Fig. 2), such as in populations from the Sierra Madre Oriental (NHgo increasing in size south to NOax). Individuals from western Mexican populations (SMS) were largest in several morphometric dimensions (BL, WC, TAIL). Although the general pattern within Mexico is of

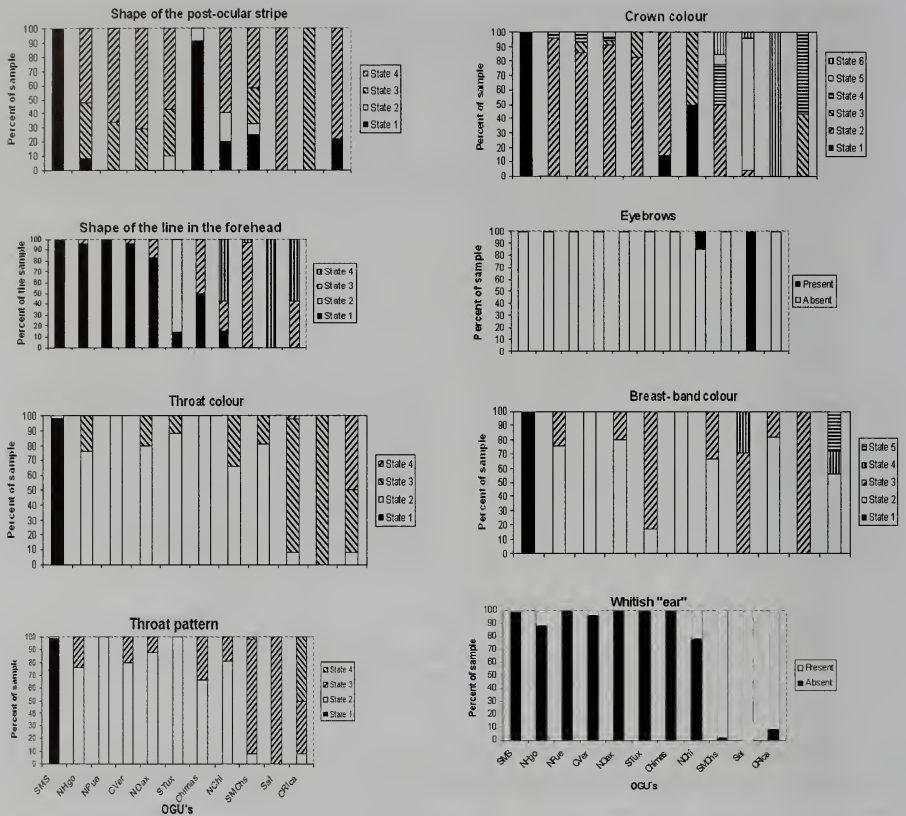


Figure 5. Frequencies of presence of coloration characters in the *Chlorospingus ophthalmicus* complex in Mesoamerica. OGU acronyms refer to those used in Fig. 1b.

increasing size southward, size decreases again in Central American populations (Fig. 2), making overall patterns more complex than simple clines.

Phenograms of morphometric characters revealed deep morphometric differentiation of SMChs from the remaining OGU's, which appear to cluster by size: smallest body size populations (NHgo, NPue, Chimas, and CRica) in one group, intermediate-size populations (STux, NOax) in a second, and largest-size populations (Sal, SMS; Fig. 3) being outgroups to the other clusters based on body size. PCA (Fig. 4) again indicated clear separation of the SMChs population; Sierra Madre Oriental populations formed a cline, with smaller populations (NHgo, NPue) in the upper part of the graph, increasing in size in CVer and NOax to Chimas, SMChs, STux and SMS, which were largest and distant from the rest of the OGU's in morphometric space.

TABLE 1

Factor loadings for the characters used in this study. Significant loadings are emboldened (>.700000).

VARIABLE	FACTOR 1	FACTOR 2	FACTOR 3
BL	-0.462186	-0.064384	0.730862
BD	-0.344410	-0.579814	0.442335
BW	-0.555169	0.648783	0.209866
WC	-0.590800	-0.552444	-0.364449
TAIL	-0.735521	-0.184918	-0.376500
TAR	-0.605233	0.547992	-0.189034
Explained Variation	1.896790	1.400933	1.084174
Proportion of Total	0.316132	0.233489	0.180696

TABLE 2

Characters defining species within the *Chlorospingus ophthalmicus* complex. Colours are from Smithe (1975).

Taxon	Crown	Throat	Breast-band	Whitish 'ear'	Eye-brow	Postocular spot	Throat pattern	Forehead spots
<i>C. postocularis</i>	Sepia	Light	Spectrum yellow	Present	Thin	Behind the eye	Speckled, no whiskers	Absent
<i>C. wetmorei</i>	Olive	Intermediate	Spectrum yellow, Chatreuse	Absent	Thin	Longer, almost surrounding all the eye	Speckled, whiskers 'washed'	Elongated white V-shaped
<i>C. albifrons</i>	Cinnamon brown	Dark	Orange yellow	Absent	Thin	Teardrop-like, almost surrounding the eye	Conspicuous whiskers, only speckled laterally	Round white spots
<i>C. dwighti</i>	Olive	Light	Chatreuse, Olive Green	Absent	Thick	Longer, almost surrounding the eye	Speckled, whiskers 'washed'	Washed
<i>C. ophthalmicus</i>	Olive	Intermediate	Spectrum yellow, Chatreuse	Absent	Thin	Longer and thinner, almost surrounding all the eye	Speckled, whiskers 'washed'	Washed

Characters of plumage coloration showed diverse patterns of variation across geography (Fig. 5). Multiple characters revealed the discrete differentiation of SMS from other populations (throat pattern and colour, breast-band colour, head colour). Single characters showed discrete breaks at other points in the distribution of the group (e.g., 'ear' colour between Chimas and SMChs, shape of the postocular spot in STux). Still other characters showed frequency variation across Mesoamerica (e.g., throat and head colours).

Discussion

Like other bird species inhabiting fragmented biomes such as cloud forests (e.g., *Myioborus miniatus*, O'Neill 1982, Pérez-Emán 2005; *Aulacorhynchus prasinus*, Navarro *et al.* 2001), significant geographic variation was detected in morphology of *C. ophthalmicus* (Remsen 1984, Isler & Isler 1987), even on the restricted geographic scale of northern Middle America. That such dramatic and discrete variation is visible *within* just one of the eight morphological groups (Isler & Isler 1987) suggests variation across the entire range of the 'species' will be even more impressive.

Size differences observed in this study generally corresponded with known geographic barriers, especially lowland interruptions to mountain chains, which delimit distributions in many montane clades (Escalante *et al.* 1993, Peterson *et al.* 1999). In Mesoamerica, the principal barriers for montane species are the Isthmus of Tehuantepec and the Nicaragua Depression, as well as the drier highlands of interior Mexico. The fairly marked differentiation amongst major mountain masses north and west of the Isthmus of Tehuantepec suggest that the early interpretation of these barriers (Peterson *et al.* 1992) was correct. Similar size differences amongst isolated montane populations occur in other taxa, such as *Aulacorhynchus prasinus* (Navarro *et al.* 2001).

Geographic variation in coloration in Mesoamerican *Chlorospingus* shows a typical 'leapfrog' pattern (Remsen 1984), with several characters present in widely separated populations but not in intermediate populations (Fig. 5). Though this pattern has been explained as similar selection pressures in widely separated areas, resulting in similar expression of characters (Remsen 1984, Fjeldså & Krabbe 1990, García-Moreno & Fjeldså 2000), it might involve evolutionary differences related to individual and species recognition (Cracraft 1983, Johnson 2002), or could be a simple consequence of evolutionary changes in intermediate populations in strings of isolated insular populations.

Studies of mtDNA sequences of Mesoamerican *Chlorospingus* populations revealed extreme levels of genetic differentiation (García-Moreno *et al.* 2004), coinciding with our previous study (Peterson *et al.* 1992) which also identified strong differentiation amongst four populations based on allozyme loci. García-Moreno *et al.* (2004) documented five well-differentiated clades in Mexico, with a clear hierarchy of relationships and segregated by clear geographic boundaries. Each has apparently been isolated genetically for significant time periods. Discrete morphological breaks documented here coincide with the phylogenetic findings: the groups from the Sierra Madre del Sur (SMS) and Sierra Madre de Chiapas (SMChs) were recovered in both analyses. Although some of the OGUs, in the Sierra Madre Oriental, Los Tuxtlas (STux) and northern Central America, were combined in a single grouping owing to size similarities, these clearly separated in the phylogenetic study. The seemingly minor (but discrete) morphological breaks documented herein coincide closely with zones of significant genetic



differentiation, in this case associated with lowlands like the Isthmus of Tehuantepec, separating the northern forms *ophthalmicus* and *albifrons* from southern *postocularis* and *dwightii*; and the Gulf slope, which separates Sierra Madre Oriental *ophthalmicus* from Los Tuxtlas *wetmorei*, or with unsuitable habitat in the Transvolcanic Belt, which separates Sierra Madre Oriental *ophthalmicus* from Sierra Madre del Sur *albifrons*. Therefore, the different *Chlorospingus* lineages in Mexico may represent species (Puerto *et al.* 2001, Helbig *et al.* 2002, Irwin 2002, Wiens & Penkrot 2002).

Species limits and taxonomy

Undoubtedly, one factor that has promoted diversification of *Chlorospingus* is its almost complete restriction to cloud forest, which has a patchy, discontinuous distribution (Fig. 1b). This geographic setting impedes gene flow between populations and has probably produced the long branches separating clades in the group (García-Moreno *et al.* 2004). The existence of marked genetic differentiation and multiple coincident morphological breaks suggests that species limits should be reassessed. Of course, genetic evidence should be used carefully when treating allopatric populations (Edwards *et al.* 2005), but this caveat should not be an excuse not to re-examine species limits in such taxa. In *Chlorospingus*, significant genetic differentiation coincides with morphometric differentiation and plumage coloration differences, at least demonstrating concordant signals amongst character sets. These data clearly indicate that the five Mexican *Chlorospingus* clades are clearly diagnosable and qualify as evolutionary or phylogenetic species (Wiley 1980, Cracraft 1983, Navarro & Peterson 2004, Watson 2005).

In general, variation in morphology and coloration was almost discrete and differences in character combinations amongst populations were abrupt. This situation avoids the problems of non-coincident variation patterns amongst character sets (Wiens & Penkrot 2002). Given the importance of plumage recognition in the breeding biology of birds and preliminary data concerning vocal variation amongst the same populations (Sosa-López 2004), we suggest these populations may also prove to be reproductively isolated and thus qualify as biological species as well. Hence, we suggest recognition of five allopatric species in northern Mesoamerica, as follows (see Fig. 6 and Table 2 for diagnostic characters). Common names are adapted from Ridgway (1902) and Winker *et al.* (1997).

Chlorospingus postocularis Cabanis, 1866. Dusky-headed Bush-tanager—extreme south-east Sierra Madre de Chiapas (Volcán Tacaná, probably west to El Triunfo) and mountains on the Pacific slope of Guatemala, Honduras, El Salvador and probably western Nicaragua. These populations form the deepest branch in the phylogeny of García-Moreno *et al.* (2004), and are also the most external clusters in our UPGMA and PCA results (Figs. 3–4). Individual samples are genetically relatively different from one another (García-Moreno *et al.* 2004) because they represent the extremes of the distribution of this form, and still

- more distinct populations may be documented (García-Moreno *et al.* in prep). This zone of differentiation coincides with distributions of other species complexes (e.g. *Atlapetes albinucha* vs. *A. gutturalis* and *Basileuterus rufifrons* vs. *B. delatitrii*), though no other complex has been studied using molecular characters. Besides the subspecies *postocularis*, this species includes populations usually assigned to the subspecies *honduratus* and *schistaceiceps*.
- Chlorospingus wetmorei* Lowery & Newman, 1949. Wetmore's Bush-tanager—montane forest and adjacent lowlands (Winker 1997) of the Sierra de los Tuxtlas, southern Veracruz. Its avifauna (and other components of its biota) represents an oft-neglected local focus of endemism (e.g. Winker 1997). This set of *Chlorospingus* populations is amongst the most genetically distinct in Mexico (García-Moreno *et al.* 2004). Other avian endemics in the region include *Buarremon (brunneinucha) apertus* (Peterson *et al.* 1992), *Campylopterus excellens* and *Geotrygon carrikeri* (Peterson 1993).
- Chlorospingus albifrons* Salvin & Godman, 1889. White-fronted Bush-tanager—Sierra Madre del Sur in Guerrero and Oaxaca (Sierra de Yucuñacua and Sierra de Miahuatlán; Binford 1989). Some Sierra Madre del Sur cloud forest islands may have been isolated for long periods and the molecular dataset suggests non-trivial differentiation of populations within this form (cf. *Eupherusa poliocerca* from Guerrero vs. *E. cyanophrys* from Sierra de Miahuatlán, which show such a pattern). However, more thorough sampling is required to assess the degree of genetic continuity in these populations (García-Moreno *et al.* in prep). This species includes populations in the Sierra de Miahuatlán, sometimes assigned to subspecies *persimilis* (Phillips 1966).
- Chlorospingus dwighti* Underdown, 1931. Dwight's Bush-tanager—montane northern Chiapas and extreme eastern Oaxaca (Chimalapas, *contra* Binford 1989) west to the Atlantic slope of Guatemala (Underdown 1931) and probably the western Sierra Madre de Chiapas.
- Chlorospingus ophthalmicus* (Du Bus, 1847). Brown-headed Bush-tanager—the Sierra Madre Oriental, from south-east San Luis Potosí south to northern Oaxaca. Specimens assigned to this form from extreme western Chiapas (Montserrate area, Miller *et al.* 1957) should be re-examined, but probably represent *C. dwighti*. Molecular studies (García-Moreno *et al.* 2004) suggest this clade may be further subdivided, with samples from northern Oaxaca vs. samples from further north (San Luis Potosí south to central Veracruz) forming distinct subclades, but further study involving more complete sampling of additional character sets is clearly needed (Sosa-López 2004).

Given that *C. ophthalmicus* under this taxonomy becomes endemic to Mesoamerica (type locality = Jalapa, Veracruz, Mexico), populations south of our study region remain to be analysed, afforded species limits and named correctly. For the present, the available name for southern Central and South American

populations with priority is *C. flavopectus* (Lafresnaye, 1840), which should be used preliminarily until the taxonomic status of southern forms is better defined.

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APPENDIX

Coloration character states and reference specimens used. Numbers in parentheses depict colour numbers as in Smithe (1975). Museum acronyms: Museo de Zoología de la Facultad de Ciencias, UNAM (MZFC); Natural History Museum, Tring, UK (NHM).

Crown colour

- State 1.—Cinnamon Brown (33) MZFC 3975
 State 2.—Olive Brown (28) MZFC 9715
 State 3.—Olive (30) MZFC 12363
 State 4.—Fuscous (21) MZFC 13112
 State 5.—Sepia (119) MZFC 8802
 State 6.—Neutral Gray (83) MZFC 7682

Shape of the line in the forehead

- State 1.—Round white spots MZFC 3975
 State 2.—Elongated V-shaped, white MZFC 7203
 State 3.—Washed MZFC 8802
 State 4.—Absent MZFC 9584

Shape of the postocular stripe

- State 1.—'Teardrop' MZFC 3975
 State 2.—Longer and thicker, almost surrounding the eye MZFC 9715
 State 3.—Longer, almost surrounding the eye MZFC
 State 4.—Only behind the eye MZFC 8802

Whitish 'ear'

- Absent MZFC 9584
 Present MZFC 3975

Throat colour

- State 1.—Dark MZFC 3975
 State 2.—Intermediate MZFC 7203
 State 3.—Light MZFC 9584

Breast-band colour

- State 1.—Orange yellow (18) MZFC 3975
 State 2.—Spectrum yellow (55) MZFC 9749
 State 3.—Chartreuse (158) MZFC 9576
 State 4.—Olive Green (48) MZFC 9584
 State 5.—Lime Green (59) + Spectrum Orange (17) NHM 85.6.8.21

Throat pattern

- State 1.—Conspicuous whiskers, only laterally speckled MZFC 3975
 State 2.—Speckled, whiskers 'washed' MZFC 9715
 State 3.—Speckled, no whiskers MZFC 8802
 State 4.—Conspicuous whiskers NHM 85.6.8.21

Head stripes

- Thin blackish MZFC 8802
 Thick, black NHM 98.12.14.573

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Nine bird species new to Bolivia and notes on other significant records

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During field studies in 2001–05 we travelled widely in northern Bolivia, from the puna of Oruro to lowland rainforest of Pando, and compiled many ornithological records, some interesting from a national or biogeographical standpoint. These include the first Bolivian records of eight species (all of them documented): Wire-crested Thorntail *Discosura popelairii*, Green-tailed Goldenthrout *Polytmus theresiae*, Ocellated Woodcreeper *Xiphorhynchus ocellatus*, Chestnut-throated Spinetail *Synallaxis cherriei*, White-cheeked Tody-tyrant *Poecilatriccus albifacies*, Sulphur-rumped Flycatcher *Myiobius barbatus*, Citron-bellied Attila *Attila citriniventris* and Pale-bellied Mourner *Rhytipterna immunda*. We also report the first documented record of Ruby-topaz Hummingbird *Chrysolampis mosquitus*, previously known from three published reports, all either dubious or provisional. In addition, we include details of the first Bolivian records of Chimney Swift *Chaetura pelagica* (undocumented), and two taxa currently considered races of Fuscous Flycatcher *Cnemotriccus fuscatus*, namely *fuscator* and *duidae*, both of which probably warrant recognition as separate species. In effect, therefore, this paper adds 12 new species to the avifauna of Bolivia.